Prescribed fire effects on the herbaceous layer of mixed-oak forests

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Abstract: In 1994, a multidisciplinary project was established to study the effects of prescribed fire on oak forests in southern Ohio. Here we describe the herbaceous layer response to fires over a 5-year period. In four study sites, treatments imposed were unburned, periodic (1996 and 1999), and annual (1996–1999) fires. Sample plots ($n = 108$) were stratified by an integrated moisture index. Species' frequencies were recorded annually, and a total of 452 species (97% native) were documented. Though species composition was significantly affected by fire, the effects were shown by ordination to be small in magnitude relative to overall compositional variation. Burned areas developed greater small-scale species richness as grasses, summer forbs, and seed-banking species increased in frequency; however, these changes were also not large in magnitude. Though a few species increased substantially via germination after fire, most common species exhibited frequency increases or decreases of <10% on burned units. Fire effects on vegetation were largely similar between annual and periodic burns and also among integrated moisture index classes. Direct fire effects on vegetation were limited by the dormant-season timing of burns and the resprouting of woody plants. Indirect effects were limited, as fires caused relatively minor changes in forest structure and resource availability in these long-unburned forests.

Résumé : Un projet multidisciplinaire a été établi en 1994 pour étudier les effets du brûlage dirigé dans les forêts de chênes du sud de l'Ohio. Dans cet article, nous décrivons la réaction de la strate herbacée après feu sur une période de 5 ans. Les traitements appliqués dans quatre sites expérimentaux comprenaient un traitement témoin non brûlé, des brûlages périodiques (en 1996 et 1999) et annuels (1996–1999). Les placettes d'échantillonnage ($n = 108$) furent stratifiées en fonction d'un indice intégré d'humidité. La fréquence des espèces a été notée à chaque année et 452 espèces (à 97 % indigènes) ont été recensées au total. Bien que la composition en espèces ait été affectée par le feu, l'ampleur des effets, tel qu'indiqué par l'ordination, était faible relativement à la variation globale dans la composition en espèces. À petite échelle, les zones brûlées ont développé une richesse en espèces plus grande à cause de la fréquence accrue des graminées, des plantes herbacées non graminéennes et des espèces dont la germination est favorisée par les perturbations. Cependant, ces changements n'étaient pas non plus très prononcés. Bien que quelques espèces aient augmenté de façon importante parce que leur germination a été déclenchée par le feu, les espèces les plus communes ont subi des augmentations ou des diminutions de fréquence inférieures à 10 % dans les zones brûlées. Les effets du feu sur la végétation étaient largement similaires que les brûlages aient été périodiques ou annuels et quelle que soit la classe d'indice intégré d'humidité. Les effets directs du feu sur la végétation ont été limités parce que les brûlages avaient été effectués durant la saison morte et que les plantes ligneuses produisaient des rejets. Les effets indirects ont été limités parce que le feu a provoqué des changements relativement mineurs dans la structure de la forêt et la disponibilité des ressources dans ces forêts qui n'avaient pas été brûlées depuis longtemps.

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Introduction

Oak–hickory is the most abundant forest type in the United States (Smith et al. 2001), but oak-dominated landscapes throughout the eastern United States are becoming more dense with shade-tolerant and fire-sensitive tree species, threatening sustainability (Lorimer 1984; Abrams 1992). Fire suppression is thought to be a primary cause of the these compositional changes, and prescribed fire has been suggested widely as a tool to sustain oak ecosystems (Brose et al. 2001; Healy and McShea 2002; Johnson et al. 2002). Indeed, several studies have shown that prescribed fire can improve oak regeneration (e.g., Kruger and Reich 1997; Brose and Van Lear 1998), and it is being used more frequently on public forest lands (Brose et al. 2001). However, relatively little is known about fire effects on the herbaceous layer vegetation in eastern deciduous forests (Gilliam and Roberts 2003b).

The herbaceous layer, composed of herbaceous and woody species, harbors the great majority of vascular plant diversity in eastern deciduous forests (Gilliam and Roberts 2003a). In landscapes with significant topographic heterogeneity, herb layer composition and diversity vary along with aspect-related gradients of microclimate and soil moisture and fertility (Hutchinson et al. 1999). Herb layer vegetation is also affected by natural and anthropogenic disturbances to the tree canopy, including individual tree falls, catastrophic wind events, and timber harvesting, which result in large increases in resource availability (Small and McCarthy 2002; Roberts and Gilliam 2003). By contrast, surface fires usually cause minor damage to overstory trees but affect herb layer vegetation directly by killing aboveground stems and indirectly by altering the forest floor and the availability of light, water, and nutrients (Gilliam 1988; Kruger and Reich 1997).

Both fire and topography can influence vegetation to varying degrees. In tallgrass prairie, Gibson and Hulbert (1987) showed that time since burning was the primary factor affecting species composition, and topographic effects were secondary. By contrast, in a longleaf pine ecosystem, woody plant communities were more strongly affected by topographic position than by fire (Liu et al. 1997). These studies also indicate that fire can either reduce (Gibson and Hulbert 1987; also see Collins 1992) or reinforce (Liu et al. 1997) differences in vegetation across the landscape.

Several studies have shown variable effects of prescribed fire on herb layer vegetation in oak forests (McGee et al. 1995; Ducey et al. 1996; Arthur et al. 1998; Franklin et al. 2003). However, to gain a broader and more general understanding of fire effects there is a need for long-term studies of different fire frequencies conducted at spatial scales that are sufficient to describe variation across the landscape.

In the unglaciated Allegheny Plateau of southeastern Ohio, strong topographic gradients support both xerophytic and mesophytic communities (Olivero and Hix 1998; Hutchinson et al. 1999; Small and McCarthy 2002). This topographic heterogeneity results in relatively high levels of landscape-level plant diversity; more than 1100 vascular plant species have been reported from a single township of approximately 10 000 ha (Cusick and Silberhorn 1977). Fires occurred frequently in southeastern Ohio forests until suppression policies were instituted in 1923 (Leete 1938; Sutherland 1997). The long-term effects of fire suppression on herb layer vegetation in this region are unknown.

In 1994, we established a multidisciplinary project to study the effects of repeated prescribed fires on oak forest ecosystems (Sutherland et al. 2003a). Over a 4-year period (1996–1999), three prescribed fire treatments were applied at each of four study sites: annual burn (four fires), periodic burn (two fires), and unburned (no fire). Also, an integrated moisture index (IMI) was used to stratify the landscape into xeric, intermediate, and mesic classes (Iverson et al. 1997). Our general hypothesis was that prescribed fire would cause significant changes to herb layer composition and diversity through the differential responses of fire-tolerant and fire-intolerant species. More specifically, we sought to answer the following questions: (*i*) Do annual and periodic burns produce different effects? (*ii*) Are fire effects different across the landscape, that is, among moisture regimes? (*iii*) Which species or species groups are most strongly affected by fire?

Materials and methods

Study area and experimental design

The study sites are located in the Southern Unglaciated Allegheny Plateau, characterized by dissected topography, high hills, sharp ridges, and narrow valleys (McNab and Avers 1994). Underlying bedrocks are primarily sandstones and siltstones, producing acidic, well-drained soils (Boerner et al. 2003). Annual precipitation, temperature, and frost-free days average 1024 mm, 11.3 °C, and 158, respectively. The region has two distinct fire seasons, spring (March–April) and fall (October–November), and nearly all fires are anthropogenic in origin (Yaussy and Sutherland 1994).

Four study sites were established in 1994. Watch Rock (77 ha; 39°12′N, 82°23′W) and Arch Rock (80 ha; 39°11′N, 82°22′W) are located in Vinton County on the Vinton Furnace Experimental Forest, owned by MeadWestvaco Corporation. Young's Branch (75 ha; 38°43′N, 82°41′W) and Bluegrass Ridge (109 ha; 38°36′N, 82°31′W) are located in Lawrence County on the Ironton Ranger District of the Wayne National Forest. The four study sites had overall similar attributes, including bedrock geology, soil, elevation, and topographic relief (Sutherland et al. 2003a). Also, forests on the four sites were similar; mean values among sites range from 25.3 to 27.8 m²/ha for tree basal area, 76%–83% for oak + hickory basal area, and 100–120 years for stand age (Yaussy et al. 2003). All sites were likely clear-cut in the mid- to late-1800s for charcoal production. Forests have since undergone secondary succession, with some stand-level canopy disturbances in the 20th century, presumably from a combination of anthropogenic (e.g., selective harvest) and natural (e.g., drought) causes (Hutchinson et al. 2003).

The experiment's design is a split-plot with prescribed fire as the whole-plot factor. In each study site (four replicate blocks), three fire treatment units (approx. 25 ha) were delineated. For the initial phase of the study (1995–1999), a control unit (hereafter "unburned") remained unburned, an infrequent burn unit (hereafter "periodic") was burned twice (1996 and 1999), and a frequent burn unit (hereafter "annual") was burned annually from 1996 to 1999.

Because of strong topographic gradients in microclimate and soil moisture, an IMI was applied to stratify the treatment units and was the split-plot factor in the design (Iverson et al. 1997). The IMI, which is based on a geographic information system, predicts relative moisture availability to plants and is derived from digital elevation model data and soil survey data. Based on calculated IMI values, each 30 m × 30 m pixel was classified as xeric, intermediate, or mesic. Iverson et al. (1997) and Iverson and Prasad (2003) provide thorough descriptions of the IMI and its application to this study.

In each treatment unit, we established three 50 m × 25 m vegetation plots in each IMI class. The vegetation plots (*n* = 108) were designed as pseudoreplicates within each IMI class per treatment unit. After establishment, plots were georeferenced, and approximately 20% had not been field-located in the intended IMI class, resulting in an uneven distribution of vegetation plots by IMI class among treatment units. However, nearly all treatment units contain two to five plots in each IMI class (Sutherland et al. 2003*a*).

Field sampling

Herb layer vegetation was sampled in half of each plot along four 25-m cross-slope transects established at 5-m intervals. Along each transect, a 1 m × 2 m quadrat was sampled at the midpoint and three 1 m × 2 m quadrats were sampled at random locations (*n* = 16 quadrats per plot). The mixture of random and semipermanent quadrats was established to compare the two methodologies. Because most quadrats (12 of 16) were randomly placed each year and the midpoint quadrats were not permanently marked (located each year with a measuring tape), the design essentially sampled different random locations per plot each year. Thus, all quadrats are treated similarly in the analyses. From 1995 to 1999, we sampled in May and again in August–September to document both spring-season and summer-season herbs. Within years, quadrat locations were the same for both sample periods. We recorded the presence of all vascular plant species that were rooted within each quadrat. Nomenclature follows Gleason and Cronquist (1991).

Prescribed fires

Prescribed fires were conducted from late March to mid-April each year. Maximum daily air temperatures ranged from 10 to 30 °C (mean = 22.1 °C), and relative humidity ranged from 20% to 50%. Most areas were burned with headfires ignited in strips ranging from several metres near firelines to >50 m in unit interiors. Flame lengths were usually less than 0.5 m, and fuel consumption was generally limited to unconsolidated leaf litter and small woody debris (1-h fuels).

Tempilaq® temperature-sensitive paints were applied to aluminum tree tags and placed in each plot to provide an estimate of fire intensity (Hutchinson 2004). Over the course of the study, recorded temperatures at 25 cm height were higher on the periodic (mean = 139 °C) than on the annual burn units (108 °C), though area burned was similar, averaging 86% and 85% on periodic and annual units, respectively.

Prescribed fires caused relatively minor reductions in overstory density (trees with diameter at breast height (dbh ≥ 10 cm), which decreased by 9.6%, 5.3%, and 2.3% on periodic, annual and unburned units, respectively (Hutchinson 2004). By contrast, sapling densities (trees 1.4 m height to 9.9 cm dbh) were greatly reduced by fire, an average of 83% and 88% on periodic and annual units, respectively (Hutchinson 2004). Unconsolidated leaf litter was also greatly reduced by fire (Hutchinson 2004). After the first fires in 1996, litter mass was reduced by 54% on periodic units and 46% on annual burn units and continued to decrease after each successive fire on the annual burn units. On the periodic burn units, litter mass returned to preburn levels by 1998, after 2 fire-free years. After the highest intensity and most complete burns in 1999, the periodic units exhibited an 85% reduction in litter.

Data analysis

Prior to analysis we selected the maximum frequency per species for each plot from the two samples taken each year. The final data set contained the absolute frequency of 452 species in 108 plots annually from 1995 to 1999 (*n* = 540 total plots). We calculated species richness (per plot and per quadrat), species diversity (Shannon Index, *H*′), and species evenness or equitability (Pielou's index, *H*′/ln(richness)) for each plot annually with PC-Ord version 4.0 (McCune and Mefford 1999). To describe treatment effects on different species groups, nine broad categories were defined: annual forbs, spring forbs (flowering in April–May), summer forbs (flowering June–October), grasses, sedges (*Carex* spp. and other Cyperaceae and Juncaceae), shrubs (included several woody vines), oak + hickory tree seedlings, shade-tolerant tree seedlings, and woody seed-banking species.

Nonparametric multiresponse permutation procedures (MRPP; McCune and Grace 2002) were performed with PC-Ord to determine whether overall species composition was significantly different among fire treatments in 1995 (pretreatment) and in 1999 (after all fires). Separate MRPP analyses were then used to determine whether the composition of each pairwise set of treatments was significantly different in 1995 and 1999. For each year, the input data set was the frequency (arcsine square-root transformed) of all species present in ≥5% of plots, and we selected the Sørenson index as the distance measure.

We used indicator species analysis (ISA, Dufrêne and Legendre 1997) in PC-Ord to identify species that were significant indicators of burned units or unburned units. Species' frequency data from all posttreatment years (1996–99) was used for the ISA, and plots were classified into unburned (*n* = 144 plots) and burned (*n* = 288 plots; annual and periodic units combined) groups. We also used ISA to determine species that were significant indicators of IMI class for all 5 years combined; groups were xeric (*n* = 170 plots), intermediate (*n* = 190), and mesic (*n* = 180). Prior to ISA, species that occurred in <3% of plots were deleted and data were arcsine square-root transformed.

To examine patterns and trends in species composition, we used the ordination method of nonmetric multidimensional scaling (NMS). To reduce noise in the species data, we deleted rare taxa (present in <3% of the 540 plot samples) and data were arcsine square-root transformed, as suggested by McCune and Grace (2002). The resulting data set contained 229 species and had much lower skewness, kurtosis, and coefficient of variation. We performed the NMS ordina-

tion (229 taxa, 540 plots) in PC-Ord with the following settings: Sørensen distance measure, a six-dimensional solution (six axes), 20 runs with data, 300 maximum iterations, an instability criterion of 0.0001, and a Monte Carlo test using 30 runs with random data. The three-axes solution exhibited the lowest mean stress and was selected as the final NMS solution. To simplify the graphical presentation of the ordination, only the 1995 (pretreatment) and 1999 (posttreatment) scores for each plot are shown in the results. Pearson product–moment correlation analysis was performed to test for significant relationships between environmental variables and 1995 and 1999 plot scores for each axis (PROC CORR; SAS Institute 1999). Included as environmental variables were pretreatment soil conditions (nitrogen mineralization rate, nitrification rate, pH, texture (see Morris and Boerner 1998)), IMI, and maximum fire temperature (only for correlation with 1999 plot scores).

We used a mixed-model analysis of covariance to test for significant treatment effects on species richness and diversity, as well as on the NMS ordination plot scores over time (PROC MIXED; SAS Institute 1999). The four study sites were treated as random block effects, with fire and IMI as fixed effects. Though quadrats were randomly placed each year, repeated measures analysis was used because the experimental units (25 m × 25 m vegetation plots) were permanent (Moser et al. 1990; Von Ende 2001). An autoregressive correlation structure within sampling units among years also provided a better description of the data, indicated by a lower –2 residual log likelihood, than assuming years to be independent. Pretreatment (1995) data were used as the covariate to test for posttreatment effects of fire, IMI, fire × IMI, and fire × year. If the overall F test was significant ($p < 0.05$) then we used post hoc least-squares means (LS-means) tests to determine significant differences ($p < 0.05$) within each year.

Results

A total of 405 species were recorded, with an additional 47 taxa identified to genus (hereafter also referred to as "species"). The species consisted of 241 perennial forbs, 58 perennial graminoids, 42 trees, 24 shrubs, 24 annual forbs, and 11 woody vines. Only 15 species were nonnative, and none of these were abundant either before or after fire treatments.

Frequency trends of common species

Prescribed fires caused relatively minor changes in the frequency of most common species (Appendix A). Of 66 common species, nine were significant indicators of unburned units (indicator species analysis, $p < 0.01$) and 20 were indicators of burned units (Appendix A). For species that were significant indicators of fire, changes in frequency over time were most often similar between periodic and annual burn treatments and remained stable on unburned units.

Several species exhibited distinct temporal dynamics in response to prescribed fire. *Erechtites hieracifolia*, an annual seed-banking forb, increased by abundant germination from <10% to >70% mean frequency on both burn treatments after the initial fires, then rapidly returned to preburn levels during fire-free years (Fig. 1a). By contrast, the annual forb *Galium aparine*, which emerges and flowers in early spring, decreased to <2% frequency on both burn treatments by

1999 while it increased to 19% frequency on unburned units (Fig. 1a). Several perennial graminoids increased in frequency on both fire treatments, for example, *Panicum commutatum* increased from <6% to >20% (1995–1999), and *Carex* spp. increased from <10% to >30% (Fig. 1b). Several perennial spring-flowering forbs in the Liliaceae family (e.g., *Smilacina racemosa*, Fig. 1c) decreased in frequency after the later (mid-April) fires in 1996, but then frequencies were similar among treatments from 1997 to 1999. The spring forb *Viola* spp. increased in frequency by >15% on both burn treatments (Fig. 1c). Several summer-flowering perennial forbs increased in frequency after fire and were significant indicators of burned sites (e.g., *Eupatorium rugosum* and *Lespedeza* spp., Fig. 1d).

Among woody plants, a number of shade-tolerant tree seedlings decreased in frequency on burned units; for example, *Acer rubrum* decreased in frequency from 60% to 40% (1995–1999) on periodic burn units and from 72% to 58% on annual burn units while remaining stable on unburned units (Fig. 1e). A few woody species that are shade-intolerant seed-bankers exhibited large increases in frequency after the initial fires (Fig. 1f). For example, *Liriodendron tulipifera* increased from <30% to >75% frequency, and *Vitis* spp. increased from <25% to >55% on both burn units from 1995 to 1996. However, these species subsequently decreased in frequency on both burn treatments from 1996 to 1999.

Community composition

MRPP indicated that overall species composition was not significantly different among fire treatment units prior to burning in 1995 ($T = 0.02$, $p = 0.42$). By 1999, after prescribed fires, MRPP indicated that species composition was significantly different among treatments ($T = –6.78$, $p < 0.001$). MRPP pairwise comparisons for 1999 data showed that the composition of unburned plots differed significantly from that of both periodic ($T = –7.66$, $p < 0.001$) and annual ($T = –7.02$, $p < 0.001$) burn plots. However, there was no significant difference in species composition between periodic and annual burns in 1999 ($T = 0.32$, $p = 0.51$).

The NMS ordination of all 108 plots from 1995 to 1999 consisted of three axes with a stress value of 10.8 and an instability criterion of < 0.001, indicating a good representation of the original distance matrix (McCune and Grace 2002). Axis 1 accounted for the greatest proportion of compositional variation ($r^2 = 0.724$), followed by axis 2 ($r^2 = 0.122$) and axis 3 ($r^2 = 0.069$). Axis 1 plot scores for 1995 (pretreatment) and 1999 (posttreatment) were highly correlated with preburn soil nitrogen mineralization rate, nitrification rate, IMI, and pH, indicating that these variables accounted for most of the overall compositional variation (Table 1). Axis 2 plot scores were correlated with IMI and soil texture, and 1999 axis 3 plot scores were significantly correlated with maximum fire temperature. Though compositional variation along axis 3 was significantly related to fire, this axis accounted for a small proportion of the total compositional variation.

The ordination of 1995 and 1999 plot scores for axes 1 and 3 show that the primary separation of plots is along the moisture–fertility gradient represented by axis 1 (Fig. 2). Along axis 3, burned and unburned plots do not form two distinct clusters by 1999, though most plots with high axis 3

Fig. 1. Temporal trends in the frequencies (mean ±1 SE) of selected species among prescribed fire treatments. Species groups shown include (*a*) annual forbs, (*b*) graminoids, (*c*) spring-flowering forbs, (*d*) summer-flowering forbs, (*e*) shade-tolerant tree seedlings, and (*f*) woody seed-bankers. Fires are indicated by the caret (^) symbol. All species shown were significant indicators of either burned or unburned units (Appendix A).
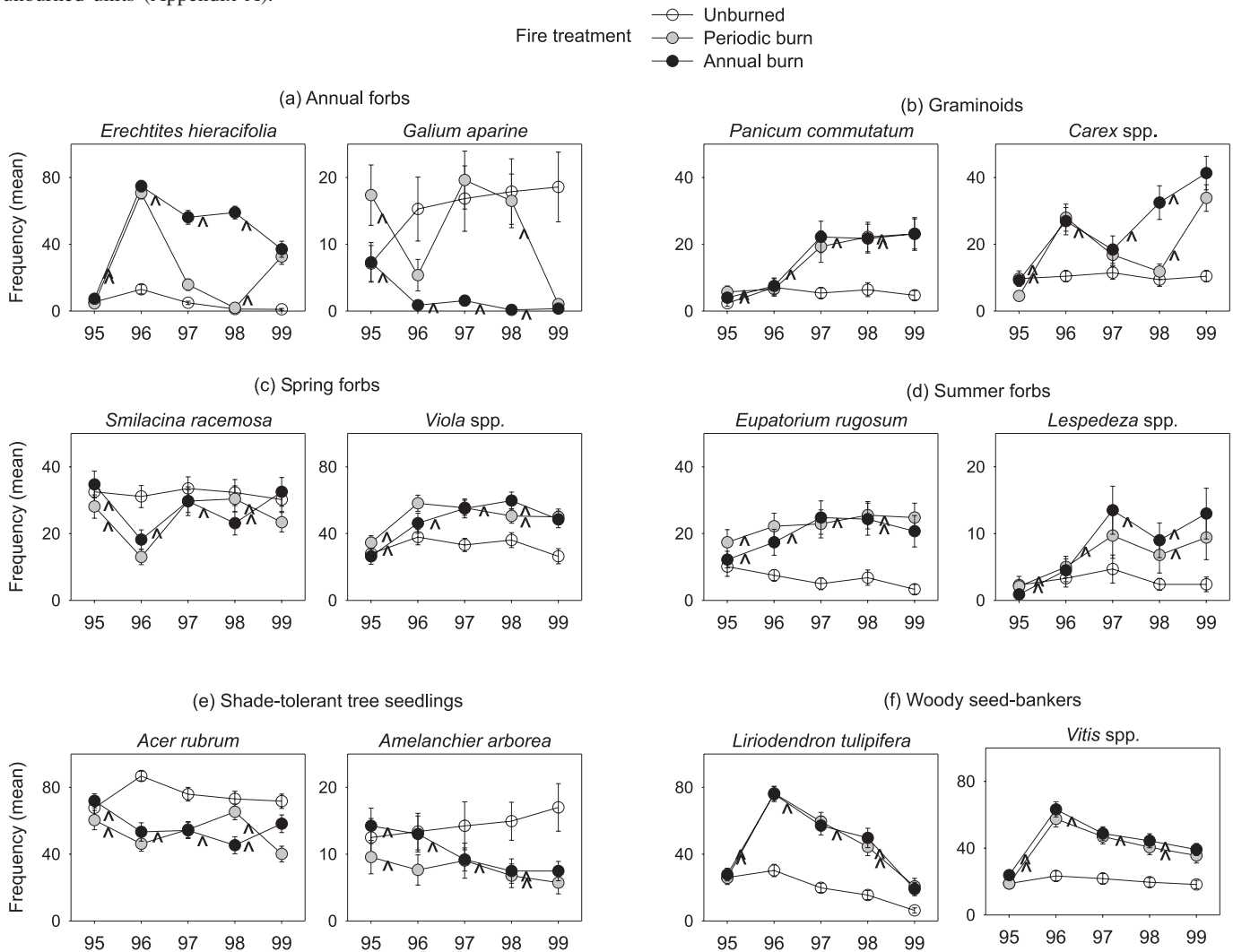
scores were burned. Also, by 1999 there is no apparent separation of annual and periodic burn plots. Analysis of covariance indicated significant effects of fire ($F = 25.4$, $p = 0.001$) and fire × year ($F = 4.7$, $p < 0.001$) and fire × IMI ($F = 4.83$, $p = 0.008$) on axis 3 plot scores. Axis 3 plot scores for all IMI classes became significantly different between burned and unburned units over time (Fig. 3). However, on xeric sites, the unburned plots were significantly different than both burn treatments each year from 1996 to 1999, and the differences between unburned and burned treatments became larger by 1999 (Fig. 3).

Species richness and diversity

Analysis of covariance indicated no significant effect of fire ($F = 0.71$, $p = 0.52$) or fire × year ($F = 0.50$, $p = 0.81$) on total species richness per plot (Fig. 4*a*). Mean plot-scale richness changed little from 1995 to 1999 on unburned units (61.8 ± 2.6 to 60.1 ± 1.4), periodic burns (67.4 ± 2.7 to 68.1 ± 2.3), or annual burns (66.3 ± 2.8 to 68.0 ± 2.6). By

contrast, fire had a significant effect ($F = 5.40$, $p = 0.04$) on total species richness per 2-m² quadrat (Fig. 4*b*). Quadrat-scale richness decreased slightly on unburned units from a mean of 15.8 ± 0.8 in 1995 to 14.9 ± 0.7 in 1999, while on periodic and annual burns richness increased slightly from 17.0 ± 0.9 to 17.9 ± 0.9 and from 17.3 ± 0.8 to 18.3 ± 0.8, respectively. LS-means tests indicated that both burn treatments had greater richness than unburned plots each year from 1997 to 1999 (Fig. 4*b*). There were no significant effects of IMI or interactions with IMI on species richness over time.

Species evenness exhibited a significant fire effect ($F = 6.48$, $p = 0.03$; Fig. 4*c*). Prior to treatments, evenness was similar among burn units. By 1998 and 1999, evenness was significantly greater on periodic burn units relative to both unburned and annual burn units (LS-means, $p < 0.05$). There was no significant effect of fire ($F = 2.0$, $p = 0.22$) or fire × year ($F = 0.83$, $p = 0.55$) on species diversity at the plot scale (Fig. 4*d*). Also, there were no significant effects of IMI or interactions with IMI on evenness and diversity over time.

Table 1. Pearson product–moment correlation coefficients of 1995 and 1999 nonmetric multidimensional scaling ordination plot scores with environmental variables measured in 1995 and also the maximum fire temperature recorded for each plot from 1996 to 1999.

Variable	Axis 1 ($r^2 = 0.724$)		Axis 2 ($r^2 = 0.122$)		Axis 3 ($r^2 = 0.069$)	
	1995	1999	1995	1999	1995	1999
N mineralization rate	–0.735*	–0.726*	0.265	0.275	–0.083	–0.151
Nitrification rate	–0.693*	–0.725*	–0.033	–0.025	–0.285	–0.281
IMI	–0.689*	–0.658*	0.623*	0.643*	–0.233	–0.287
pH	–0.650*	–0.668*	0.008	0.009	–0.366	–0.375
Sand	–0.053	–0.100	–0.579*	–0.580*	–0.302	–0.257
Silt	0.027	0.072	0.573*	0.571*	0.273	0.238
Clay	0.031	–0.003	–0.497*	–0.487*	–0.187	–0.172
Max. fire temperature	na	–0.055	na	–0.195	na	0.451*

Note: Bonferroni-adjusted p values were calculated for each year by $\alpha = 0.05/24$; significance is indicated with an asterisk when $p < 0.002$. For each axis, r^2 values indicate the correlation of axis plot scores with values in the original distance matrix for all 5 years, which represents the proportion of compositional variation accounted for by each axis.

Richness of species groups

Analysis of covariance indicated significant fire and (or) fire × year effects on the quadrat-scale richness of six species groups (Fig. 5). Among herbaceous groups, there were significant fire ($F = 12.74$, $p < 0.001$) and fire × year ($F = 9.95$, $p < 0.001$) effects on annual forb richness (Fig. 5a). In 3 of 4 post-burn years, annual forb richness was significantly greater on both burned treatments than on unburned treatments (LS-means, $p < 0.05$). For perennial forbs there was a significant fire × year effect on the richness of spring-flowering species ($F = 0.34$, $p = 0.01$; Fig. 5b), but within years there were no significant differences among treatments. There was a significant fire effect on the richness of summer-flowering forbs as both burn treatments had greater richness than unburned treatments each year from 1996 to 1999 (LS-means, $p < 0.05$; Fig. 5c). For graminoids, there was a significant fire effect on the richness of grasses ($F = 5.45$, $p = 0.04$; Fig. 5d) but not sedges ($F = 3.01$, $p = 0.12$; Fig. 5e). By 1999, grass richness was significantly higher on both burn treatments than on unburned units (LS-means, $p < 0.05$).

Among woody plant groups, there were no significant effects of fire ($F = 0.92$, $p = 0.45$) or fire × year ($F = 0.94$, $p = 0.47$) on shrub richness (Fig. 5f). Richness of oak–hickory seedlings exhibited a significant fire × year effect ($F = 2.35$, $p = 0.04$; Fig. 5g); richness was significantly lower on both burn treatments relative to unburned units in 1999 (LS-means, $p < 0.05$). Shade-tolerant tree seedling richness exhibited significant fire ($F = 16.82$, $p < 0.001$) and fire × year ($F = 5.00$, $p < 0.001$) effects (Fig. 5h). Shade-tolerant seedling richness was lower on both burn treatments relative to unburned units in each year from 1996 to 1999 (LS-means, $p < 0.05$). The richness of woody seed-banking species was significantly affected by fire ($F = 11.55$, $p < 0.001$), as richness was greater on both burn treatments relative to unburned units each year from 1996 to 1999 (Fig. 5i).

Discussion

Over a 5-year period, the herbaceous layer vegetation of mixed-oak forests was not greatly altered by repeated prescribed fires. Though species composition and richness were significantly affected by burning, the magnitude of effects was generally small. Overall species composition became different in burned areas than in unburned areas, as indicated by MRPP. However, ordination showed that fire contributed much less than topo-edaphic factors to overall compositional variation. Burned areas also developed greater small-scale species richness than that of unburned areas, but mean differences were only on the order of two species per 2-m² quadrat. Moreover, relatively few species exhibited large changes in frequency after fire, as most common species' frequencies changed by <10% on burned sites from 1995 to 1999.

The changes in composition and richness that were observed resulted from several species groups that were affected by fire. Seed-banking species, including several woody shade-intolerant species and the annual forb *Erechtites hieracifolia*, exhibited abundant germination after fire. Germination was facilitated, as fire consumed much of the unconsolidated leaf litter on the forest floor. Seeds of some species require light for germination (Baskin and Baskin 1988), and a dense litter layer inhibits light penetration to seeds. However, these species' responses were mostly ephemeral, as frequencies tended to decrease subsequently on both annual and periodic fire treatments after the initial burns. This pattern suggests that for the woody shade-intolerant species, repeated fires that kill newly emerged seedlings or single fires that cause only minor changes in light availability result in an ephemeral response. Also, the seed banks of these species could have become less abundant after repeated fires.

A larger group of perennial herbs, primarily grasses and summer forbs, exhibited increased frequencies after fire that may result in longer term changes in composition and richness. Because these species frequently flower and produce seed under closed- to partially open-canopy conditions, frequency increases may have resulted from both seed-bank germination and (or) increased seed production and establishment after fires. Summer-flowering herbs should benefit more than spring-season herbs from even minor increases in light availability after fire because of greater light capture over a longer period (Sparling 1967).

Fig. 2. Nonmetric multidimensional scaling ordination diagram of axes 1 and 3 for all plots (*n* = 108) in 1995 (pretreatment) and 1999, after two fires on periodic burn units and four fires on annual burn units. Environmental factors that were significantly correlated with plot scores along axis 1 or 3 are indicated in parentheses.
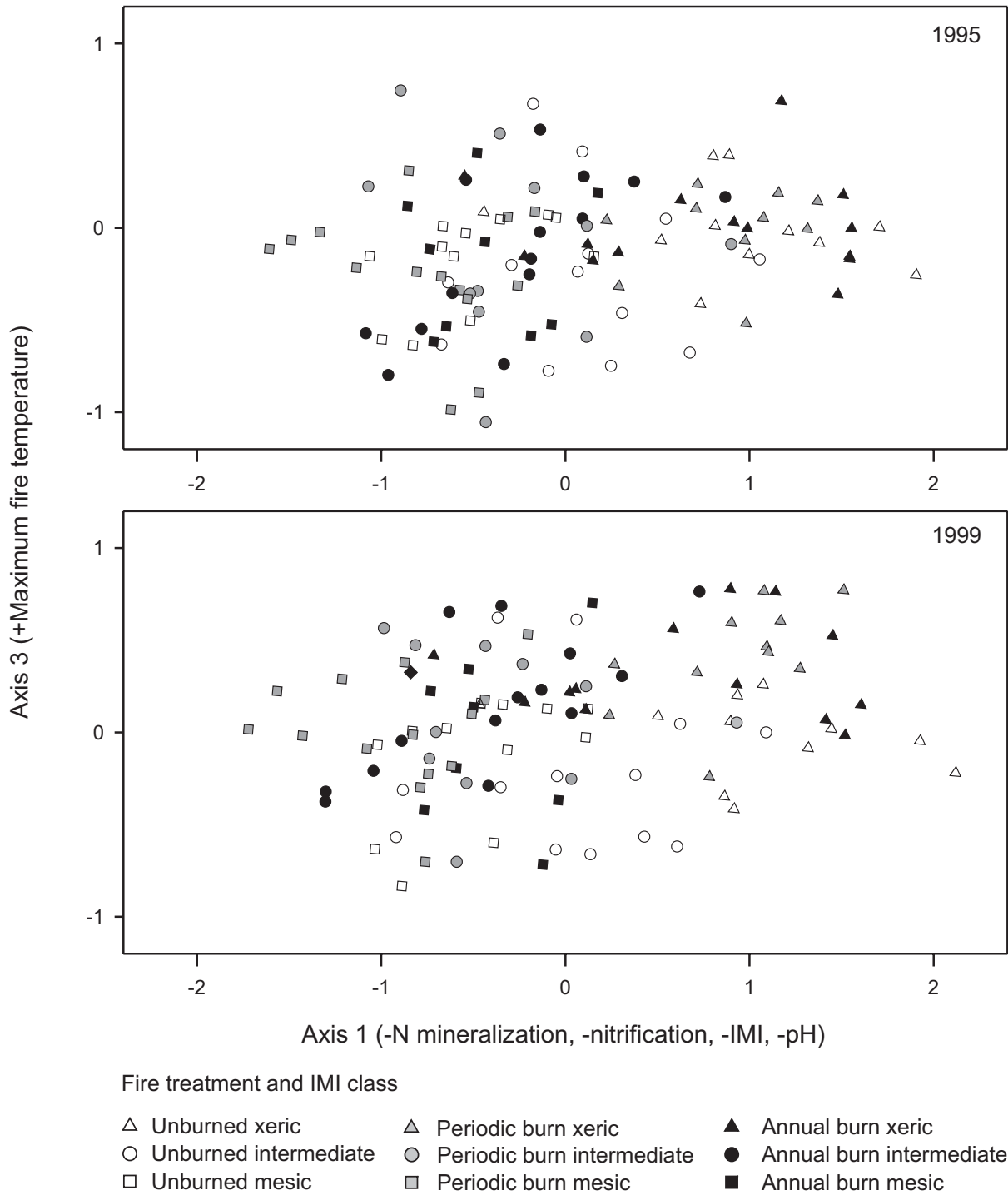
In contrast, tree seedlings, particularly shade-tolerant species, decreased in richness, and several species exhibited moderate decreases in frequency. Though nearly all tree species in our region can resprout after fire (Sutherland et al. 2000), the capacity to do so is dependent on belowground carbohydrate reserves, which varies among species (Brose and Van Lear 1998). Oak and hickory seedlings tended to decrease in frequency to a lesser extent than shade-tolerant species, which are most often small seeded and have lower root:shoot ratios and thus a lesser capacity to resprout (Sutherland et al. 2000).

The relatively small magnitude of fire effects on herb layer vegetation was likely attributed to several factors. First, the dormant-season surface fires caused minor direct injury to the most diverse group of species, the perennial herbs, most of which had not emerged when fires were conducted in late-March and early April. Fires also had low residence

Fig. 3. Analysis of covariance testing for significant differences in nonmetric multidimensional scaling ordination axis 3 plot scores among fire treatments for (*a*) xeric, (*b*) intermediate, and (*c*) mesic plots. Bars for 1996–1999 represent posttreatment least-square means (LS-means) (±1 SE) adjusted by 1995 (pretreatment) values. For 1995, bars represent means ± 1 SE. Significant annual differences among fire treatments (LS-means, $p < 0.05$) are indicated by different letters. Fires are indicated by the caret (^) symbol.

time and raised mineral soil temperature an average of only 9.3 °C at 1 cm depth during the fires and thus likely caused very little damage to rhizomes (Iverson and Hutchinson 2002). In addition, nearly all woody species can resprout after topkill, and many exhibited relatively minor changes in frequency. Moreover, the fires did not cause large changes in light availability (Hutchinson 2004), soil moisture (Iverson and Hutchinson 2002) or soil nitrogen availability (Boerner et al. 2004).

Similar to our findings, several studies in mixed-oak forests have shown that the effects of low-intensity fires on herb layer composition and diversity were small in magnitude (McGee et al. 1995; Arthur et al. 1998; Kuddes-Fischer and Arthur 2002; Franklin et al. 2003). By contrast, low-intensity fires did increase species richness more substantially in an Illinois sand forest dominated by *Quercus velutina* (Nuzzo et al. 1996), and both Ducey et al. (1996) and Elliot et al. (1999) reported that species diversity was significantly increased in areas where fire intensity was high enough to create canopy openings. As well, most of these studies found that herbaceous cover increased significantly after prescribed fire. Though not measured here in this study, herbaceous cover in 2002 was approximately three times greater (mean = 16.2%) in annual burn stands than in unburned stands (mean = 5.0%) within these same study sites (Hutchinson 2004).

In more open-structured oak barrens communities in Illinois, Taft (2003) found that prescribed fire caused substantial increases in herb layer richness, diversity, and cover over a 6-year period even though the overstory stratum was largely unaffected. As in our study, Taft (2003) also reported that C_3 graminoids, particularily *Panicum* spp. and *Carex* spp. increased on burned sites. Also, a Tennessee oak barrens community exhibited large fire effects over a 25-year period of fire treatments, as burned sites developed much greater cover and richness of grasses and forbs and unburned sites became depauperate of herbs as woody species increased in dominance (DeSelm and Clebsch 1991). In Minnesota oak savannas, Tester (1989) found that the long-term (20-year) application of prescribed fire caused substantial increases in the abundance of prairie grasses, forbs, and shrubs, while nonprairie species decreased in abundance. Leach and Givnish (1999) also reported fire-maintained oak savannas in Wisconsin exhibited the highest species diversity among plant community types in their region.

Long-term prescribed fire application also has been shown to have a large effect on herb layer vegetation in longleaf pine savannas of the southeastern United States (Brockway and Lewis 1997; Glitzenstein et al. 2003), as fire promoted greater cover and diversity of grasses and forbs. In the Missouri Ozarks, prescribed fire also promoted greater herbaceous abundance and diversity in restored shortleaf pine stands (Sparks et al. 1998). However, similar to our findings, long-unburned pine
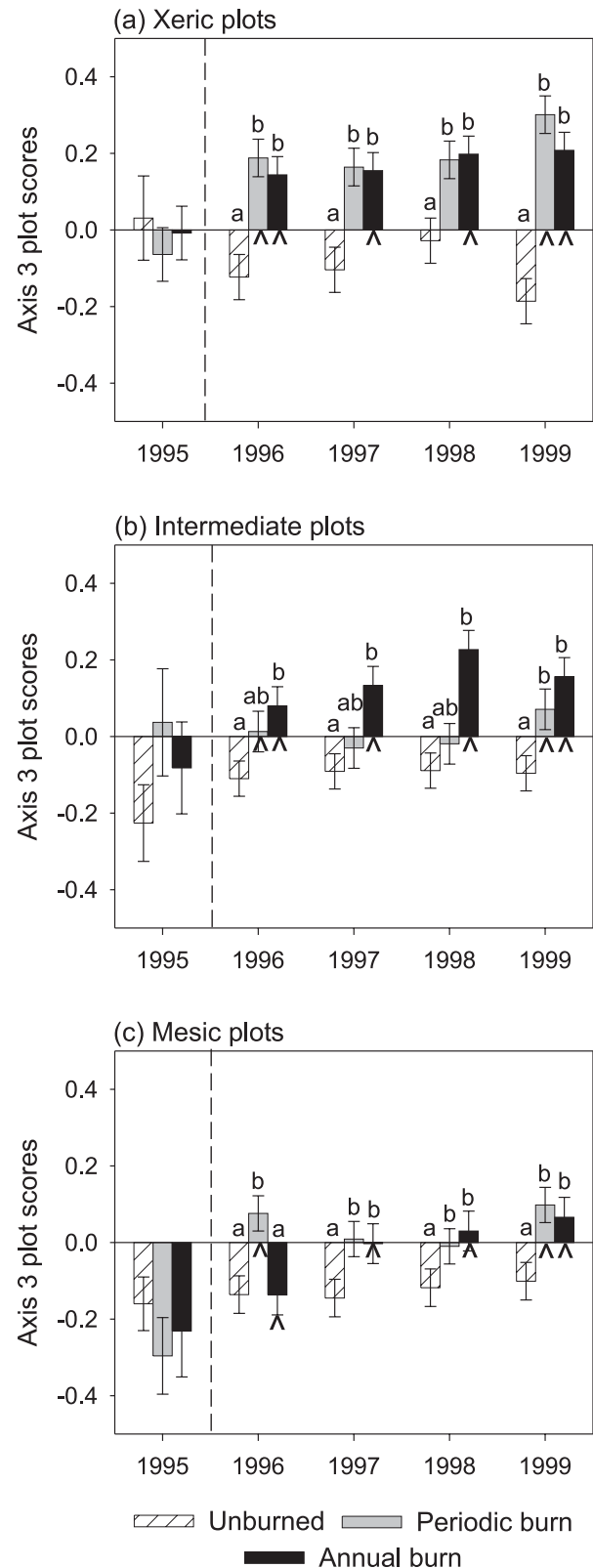
and scrub communities on the Lake Wales Ridge of Florida were largely resistant to change after fire (Abrahamson 1984; Abrahamson and Abrahamson 1996).

In our 5-year study, annual (four fires) and periodic (two fires) burns produced similar changes in species composi-

Fig. 4. Analysis of covariance testing for significant differences among fire treatments for (*a*) species richness per plot, (*b*) species richness per 2-m^2 quadrat, (*c*) Pielou's evenness index, and (*d*) Shannon diversity index. Bars for 1996–1999 represent posttreatment least-square (LS-means) (±1 SE) adjusted by 1995 (pretreatment) values. For 1995, bars represent means ± 1 SE. Significant annual differences among fire treatments (LS-means, *p* < 0.05) are indicated by different letters. Fires are indicated by the caret (^) symbol.
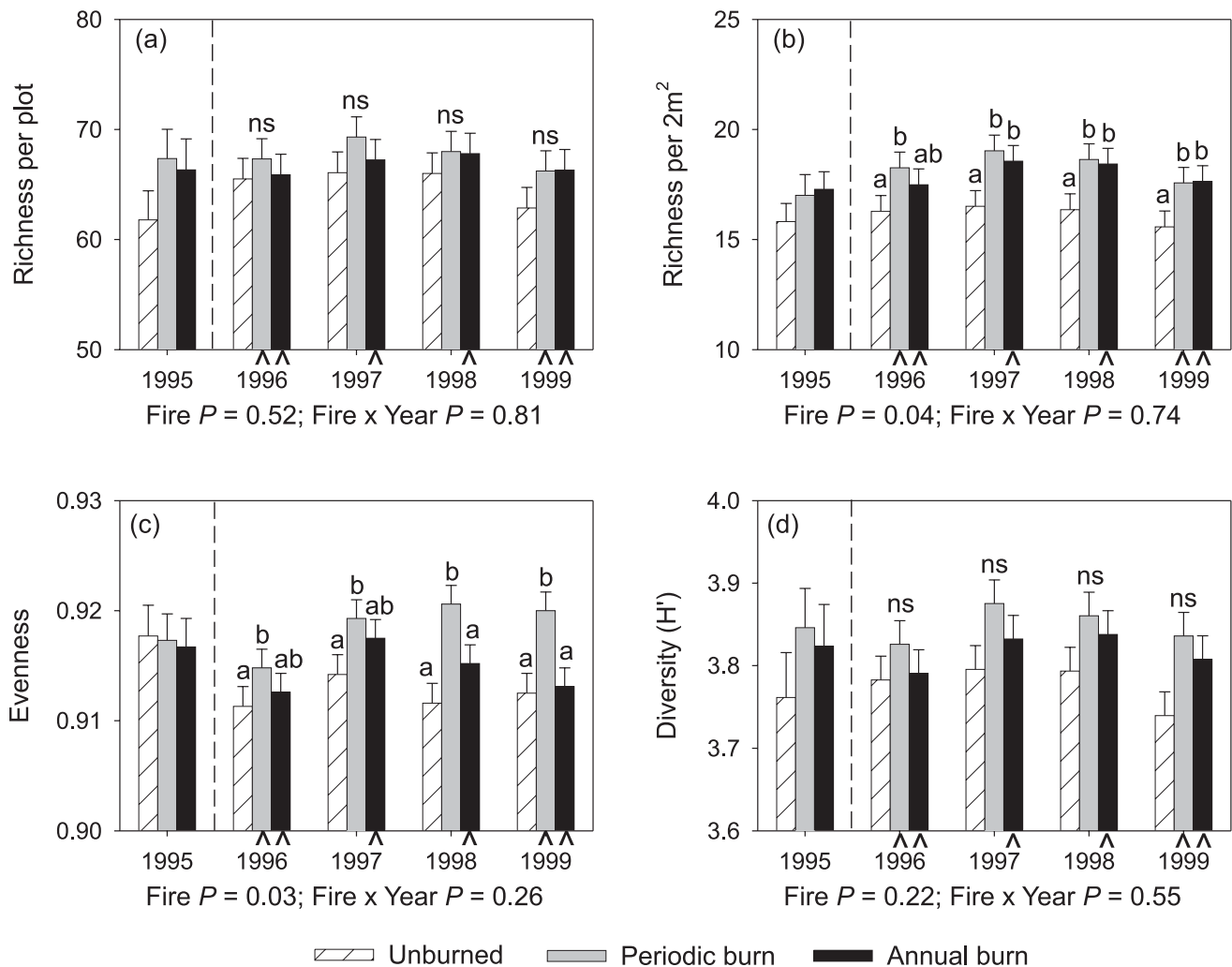

tion, total species richness, and the richness of major species groups. The similar effects likely result from the short-term nature of the treatments that also produced largely similar effects on the forest ecosystem. Annual fires had a greater cumulative effect on the abundance of leaf litter, while periodic units burned at greater intensity in 1999. However, both fire treatments caused low levels of overstory mortality, high levels of sapling mortality, exposed the humus layer and mineral soil, and resulted in similar changes in soil nutrient availability (Boerner et al. 2004). The few long-term studies of fire frequency in eastern ecosystems indicate that long-term application of different fire frequencies can produce much greater differences in ecosystem structure and vegetation (Tester 1989; Brockway and Lewis 1997; Peterson and Reich 2001; Glizenstein et al. 2003).

More surprisingly, we also found that fire effects were similar across the topographic gradient of soil moisture and fertility, represented by the IMI. Prior to burning, compositional variation was most strongly correlated with the topographic moisture–fertility gradient produced at the local watershed scale (Hutchinson et al. 1999). Also prior to burning, species

richness and diversity increased significantly from xeric to mesic landscape positions (Sutherland et al. 2003*b*). While ordination indicated that xeric plots had somewhat greater compositional change than intermediate and mesic plots, all IMI classes exhibited fire effects that were significant but nonetheless comprised only a small proportion of the total compositional variation. Though there were significant effects of fire on species richness and the richness of several species groups, there were no significant fire × IMI interactive effects over time. The similar vegetation responses across the moisture gradient resulted in part from seed-banking species that increased in frequency and tree seedlings that decreased in frequency across all IMI classes. In addition, we found no evidence that repeated fires caused a "xerification" of herb layer vegetation, as most common xeric and mesic indicator species exhibited relatively minor change after fire.

In longleaf pine ecosystems, studies have shown that strong topographic gradients in composition and diversity remain even with long-term frequent burning regimes (Kirkman et al. 2001; Glitzenstein et al. 2003). In contrast to our study, Liu et al. (1997) found larger differences in fire intensity and

Fig. 5. Analysis of covariance testing for significant differences among fire treatments for species richness per 2-m² quadrat for nine species groups (5*a*–5*i*). The number of species represented by each group is shown in parentheses. Bars for 1996–1999 represent posttreatment least-square (LS-means) (±1 SE) adjusted by 1995 (pretreatment) values. For 1995, bars represent means ± 1 SE. Significant annual differences among fire treatments (LS-means, $p < 0.05$) are indicated by different letters. Fires are indicated by the caret (^) symbol.
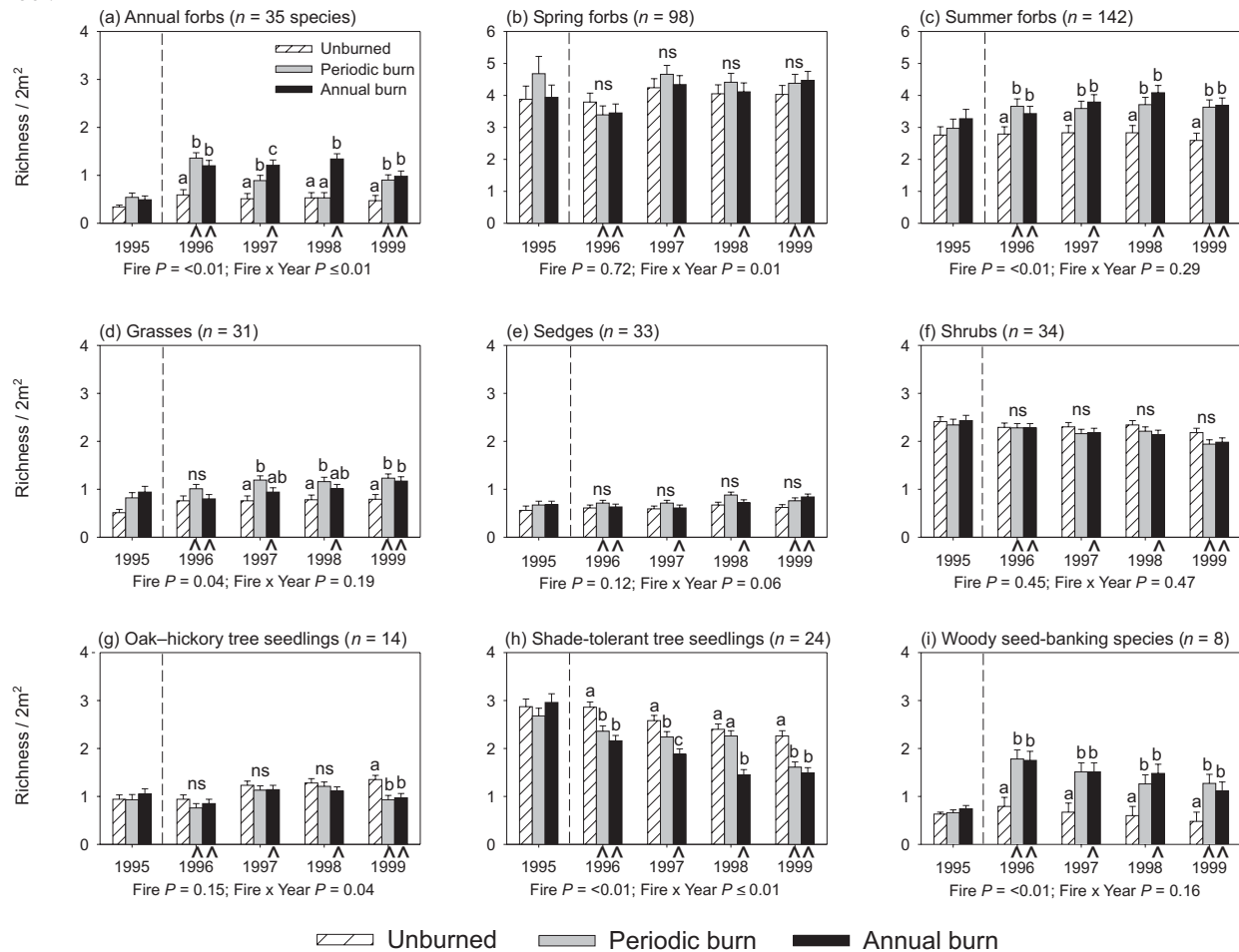
effects across a steep moisture gradient in the Big Thicket region of southeastern Texas, suggesting that fire reinforces topographic gradients in composition.

Our study was one of the few large-scale replicated studies of fire effects on herb layer vegetation in eastern forests that also incorporated topographic factors into the design. However, the sampling methods limited our ability to detect change in several important respects. First, we measured only species presence and absence in quadrats and did not estimate cover or dominance. Subsequent sampling on these study sites has shown that some species and species groups that did not show large differences in frequency or richness among treatments did exhibit substantial differences in cover (Hutchinson 2004), which has also been shown in other studies. Also, we sampled different random quadrats each year. Permanent quadrats can detect change better than random quadrats by limiting variability, particularly in communities such as ours that are dominated by perennials (Lesica and Steele 1997).

In oak-dominated forests, prescribed fire is most often applied to improve oak regeneration. Our results indicate that repeated fires do not cause large changes in herb layer vege-

tation and can increase the small-scale richness of native herbaceous species without facilitating the invasion of exotic species. After decades of fire suppression, thinning combined with prescribed fire may be much more effective in promoting oak regeneration than fire alone (e.g., Brose and Van Lear 1998). By creating more heterogeneous light levels on the forest floor, thinning and fire would likely have a more substantial effect on herb layer composition and diversity in oak forests. However, the use of fire, especially if intense or coupled with thinning, could facilitate disturbance-adapted exotic species, as studies have shown in western ponderosa pine forests (Crawford et al. 2001; Griffis et al. 2001) and several community types in California (Keeley et al. 2003). Spring-season fires (late-April and May) can improve oak regeneration to a greater extent than dormant-season fires by having a more significant impact on competing tree species (Brose and Van Lear 1998). Spring-season fires conducted after the emergence of most herbaceous species and the leafing-out of most woody species would likely also have a more substantial effect on herb layer vegetation. Future research that addresses fire coupled with silvicultural treatments, fire seasonality, and the longer term effects of

different fire regimes will be particularly useful to gain a better understanding of how different fire management practices affect herbaceous layer vegetation in oak forests.

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Appendix A

Table A1. Biennial mean frequencies of 66 common species among prescribed fire treatments.

				Unburned			Periodic burn			Annual burn		
	LF	IMI	Fire	1995	1997	1999	1995	1997	1999	1995	1997	1999
Acer rubrum	t	x	u	67.7	75.9	71.7	60.4	54.7	40.1	71.9	54.2	58.2
Acer saccharum	t	m		16.3	15.5	12.2	22.6	8.3	9.7	20.5	7.5	9.7
Amelanchier arborea	t	x	u	12.5	14.2	17.0	9.5	9.0	5.7	14.2	9.2	7.5
Amphicarpaea bracteata	f		b	15.6	12.3	12.0	17.2	27.1	20.3	24.7	25.3	22.7
Anemonella thalictroides	f	m		24.5	26.0	22.2	28.0	28.3	29.0	21.5	23.1	22.2
Arisaema triphyllum	f	m		13.7	8.9	9.0	20.3	16.1	20.0	17.9	18.6	17.2
Asarum canadense	f	m		10.8	10.9	10.2	14.6	12.0	9.0	12.5	10.9	11.1
Aster divaricatus	f	m		15.5	14.8	14.6	8.9	11.1	8.5	11.8	13.5	11.6
Brachyelytrum erectum	g		b	7.5	9.5	11.5	21.0	25.0	23.1	21.5	25.5	31.3
Carex gracilescens	g	m		9.9	9.5	12.8	10.4	14.9	14.9	11.5	12.3	15.1
Carex willdenowii	g	x		12.8	14.8	15.1	13.9	9.7	10.2	11.6	10.8	11.6
Carex spp.	g		b	9.7	11.5	10.4	4.5	16.8	33.9	9.2	18.4	41.3
Carya glabra	t	x		13.0	12.5	16.7	15.6	8.9	11.5	16.8	17.0	15.3
Cercis canadensis	t	i		15.6	14.6	11.8	15.6	15.3	14.2	17.5	17.5	16.7
Circaea lutetiana	f	m	b	4.5	4.5	4.7	13.2	10.4	12.2	9.0	9.4	9.0
Cimicifuga racemosa	f	m		14.4	14.9	14.6	14.2	14.9	16.0	15.1	17.0	16.5
Cornus florida	t	x	u	41.3	25.2	10.8	34.4	21.5	9.2	34.7	20.0	5.9
Dentaria laciniata	f	m		16.1	18.2	18.9	17.5	40.5	39.9	9.5	10.9	30.2
Desmodium glutinosum	f	i		11.1	9.5	7.5	10.8	9.9	9.7	12.3	11.3	13.0
Desmodium nudiflorum	f	i		45.0	44.3	37.2	40.8	38.5	33.7	46.7	46.4	43.8
Dioscorea quaternata	f	m		12.2	11.3	10.8	10.8	8.7	10.4	14.2	15.3	13.9
Erechtites hieracifolia	f		b	5.4	4.9	1.0	4.5	15.8	32.6	7.3	56.1	37.0
Eupatorium rugosum	f	m	b	10.1	5.0	3.3	17.4	22.9	24.8	12.2	24.8	20.7
Fraxinus americana	t	i	u	34.0	32.8	28.3	34.5	25.5	19.1	35.9	22.7	14.4
Galium aparine	f	m	u	7.1	16.8	18.6	17.4	19.6	1.0	7.3	1.6	0.3
Galium circaezans	f	m	b	19.1	17.4	17.0	25.0	28.0	30.6	30.6	29.2	33.3
Galium triflorum	f	m	b	21.0	25.3	20.0	29.7	47.2	38.9	30.9	40.3	35.9
Geranium maculatum	f	m		33.3	30.0	29.5	39.1	32.6	32.5	32.5	29.5	27.1
Helianthus divaricatus	f	x	b	4.9	4.3	2.8	4.0	6.8	6.3	6.9	9.2	7.3
Hydrangea arborescens	s	m		11.1	10.9	9.0	8.0	8.5	6.6	6.9	7.5	8.7
Lespedeza spp.	f	x	b	2.3	4.7	2.4	2.1	9.7	9.4	0.9	13.5	13.0
Lindera benzoin	s	m		11.8	12.5	12.2	20.8	22.9	16.7	13.7	10.1	9.0
Lireodendron tulipifera	t	m	b	26.0	19.8	6.3	25.7	59.5	20.7	27.8	57.1	19.1
Nyssa sylvatica	t	x		20.3	17.2	14.8	14.1	12.7	14.2	20.5	21.9	15.3
Osmorhiza claytonii	f	m	u	8.5	10.2	9.0	10.4	8.2	7.1	7.8	4.0	1.7
Panicum boscii	g	x	b	8.3	9.9	11.1	11.1	21.9	26.0	19.1	21.4	33.5
Panicum commutatum	g	x	b	2.3	5.4	4.7	5.7	19.3	23.1	4.0	22.2	23.1
Panicum dichotomum	g	x	b	3.5	3.6	4.7	6.3	11.8	12.3	6.1	8.5	14.2
Parthenocissus quinquifolius	s	i		41.3	34.9	32.5	40.3	31.1	25.9	36.8	34.7	25.5
Pilea pumila	f	m	b	3.6	4.0	2.8	11.5	13.2	13.7	4.3	6.4	8.0
Polystichum acrosticoides	f	m		20.7	20.7	21.2	19.1	20.7	20.7	20.0	21.5	22.0
Polygonatum biflorum	f	x	u	17.2	14.9	17.9	11.5	11.8	10.6	15.8	15.1	15.3
Poa cuspidata	g			12.2	13.0	11.5	14.6	17.9	13.2	19.1	14.9	11.8
Potentilla spp.	f	x		15.8	18.1	21.5	13.4	20.3	18.2	15.5	17.2	20.8
Prenanthese spp.	f	m		17.1	15.6	12.8	15.2	17.0	13.9	12.2	14.1	9.2
Quercus alba	t	x		21.7	33.3	37.5	23.1	38.2	30.9	29.9	40.6	36.3
Quercus prinus	t	x		15.5	20.3	24.0	12.2	14.9	12.8	11.6	14.4	12.3
Quercus velutina	t	x		11.6	16.8	14.1	14.4	14.4	12.3	14.9	18.2	13.7
Rosa carolina	s	x		12.2	10.9	9.0	12.2	8.9	9.5	16.0	16.1	16.7
Rubus spp.	s	i	b	17.9	21.5	20.5	21.7	37.5	44.6	22.6	44.8	42.4
Sassafras albidum	t	x	b	36.1	31.3	34.0	37.7	38.5	39.9	34.4	43.4	41.5
Sanicula spp.	f	i		8.5	9.4	8.5	15.5	19.1	15.8	16.8	18.4	16.0
Scutellaria spp.	f	m		14.4	15.3	13.0	11.1	10.1	15.1	9.2	10.9	8.5
Smilacinia racemosa	f	i	u	32.5	33.5	30.2	28.1	39.7	23.4	34.7	29.7	32.5

Table A1 (*concluded*).

	LF	IMI	Fire	Unburned			Periodic burn			Annual burn		
				1995	1997	1999	1995	1997	1999	1995	1997	1999
Smilax glauca	s	x		33.5	27.8	28.3	25.5	22.2	25.5	29.7	32.3	36.3
Smilax rotundifolia	s	x		39.9	37.3	39.8	40.6	38.2	35.6	41.3	36.1	33.5
Solidago caesia	f	i		8.5	6.6	13.2	10.4	11.1	12.3	16.7	17.2	20.3
Tiarella cordifolia	f	m		14.6	14.8	13.4	11.5	10.6	10.1	11.1	12.7	10.2
Trillium grandiflorum	f	m		20.5	22.0	23.6	17.7	18.2	18.6	15.3	15.3	14.8
Ulmus rubra	t	i		18.2	16.0	14.1	24.0	22.0	13.0	18.2	13.4	6.6
Uvularia perfoliata	f	i		39.2	36.8	36.1	19.3	19.8	19.8	38.5	34.9	37.8
Vaccinium pallidum	s	x		18.8	18.6	17.9	19.3	19.8	19.8	22.7	23.8	22.7
Viburnum acerifolium	s	m	u	28.8	32.1	29.5	25.2	23.1	19.3	21.4	16.1	16.3
Viola spp.	f	m	b	28.0	33.2	26.4	34.5	55.4	50.0	26.4	55.0	48.4
Viola palmata	f	i	b	18.9	12.0	12.7	25.9	19.1	28.1	22.6	14.9	32.5
Vitis spp.	s	x	b	18.8	21.7	18.2	18.8	46.9	35.6	23.8	48.8	39.2

Note: Common species are defined as having a mean frequency of ≥5% in any integrated moisture index (IMI) class or fire treatment over the course of the study. Life forms (LF) are indicated as follows: t, tree; s, shrub; f, forb; g, graminoid. Species that were significant indicators ($p < 0.01$) of IMI classes by indicator species analysis are indicated as follows: x, xeric; i, intermediate; m, mesic. Species that were significant indicators of fire treatment are indicated by "u" and "b" for unburned and burned units, respectively.